THE ORIGIN AND DISTRIBUTION OF THE FAMILY MYRTACEAE

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In the study of the lower eocene flora of the Mississippi embayment, a rather exhaustive compilation was undertaken to show the geological distribution of the genera present in that flora and the geographical distribution of the existing species in the families that were represented. This laborious work fully repaid the time involved, since many facts of general interest came to light and many highly suggestive, even if unproved, ideas emerged from the statistical tables.

A preliminary and somewhat tentative sketch of these matters was published,[1] and it is planned to elaborate the subject further in the final publication on the lower eocene flora under the auspices of the U.S. Geological Survey.

Among the various families that are represented in numerous fossil floras, none has excited greater interest among students of recent floras and geographical distribution than the family Myrtaceae, which in the genus *Eucalyptus* and its more immediate allies is so prominent an element in the present flora of Australia. What may be legitimately expected when fossil and recent floras shall have been studied in a sufficiently broad way, even with the present insufficient data of both recent and fossil geographical distribution, may be illustrated by the following brief sketch of what is known of the Myrtaceae.

The family Myrtaceae contains over 3100 existing species, separated by taxonomists into two subfamilies. The first of these, the Myrtoideae, with 32 genera and about 2400 existing species, comprises mostly tropical forms, of which over 75 per cent are confined to the Western Hemisphere. There are, however, over 200 species in Asia, one of which extends into Europe; about 75 species in Africa; about 200 species in Australia; and about 60 species in Oceanica. Nineteen of the genera are confined to

[1] Proc. Amer. Phil. Soc. 53:129–250. 1914.

America, and these include the only monotypic genera in the subfamily (*Orthostemon* Berg, *Psidiopsis* Berg, and *Paivaea* Berg), as well as the large and greatly differentiated genera like *Myrcia* DC. with about 450 existing species. The two other large genera, *Myrtus* Linn. with about 178 existing species, and *Eugenia* Linn. with about 1300 existing species, are the only two genera found on all the continents (except Europe), and in these two genera America furnishes 135 species of *Myrtus* and about 850 species of *Eugenia*, or over 75 per cent in *Myrtus* and over 65 per cent in *Eugenia*.

The second subfamily, the Leptospermoideae, comprises the Leptospermae with 28 genera and about 700 existing species, and the Chamaelaucieae with 12 genera and about 165 existing species. Both of these tribes are even more strikingly Australian than the Myrtoideae are American. The Chamaelaucieae are entirely Australian and are mainly confined to Western Australia, and in accordance with their peculiar habitat, specialized characters, and restricted range, are probably of relatively recent origin. The Leptospermae have a single monotypic genus in Chile, and the distribution of the other members of this tribe suggests the probability that the South American genus should be placed in some other alliance, since with the exception of *Metrosideros* Banks, which is represented in Africa, and the genus *Baeckea* Linn., which reaches the Asiatic mainland, all of the genera are confined to Australia or to the surrounding islands southeast of Asia.

ANDREWS,[2] in a recent paper, has presented some interesting statistics of distribution and an ingenious theory of the history of the family. He considers that the original stock was arborescent or shrubby, with entire, simple, opposite, penni-veined leaves with dots and intramarginal acrodrome veins; with the calyx lobes and petals imbricate, probably in fives; flowers regular, solitary or in cymes; stamens indefinite, numerous, free, with versatile, 2-celled anthers; ovary inferior, with two or more cells; style simple; fruit inferior, crowned with persistent limb of calyx, indehiscent, succulent or fleshy (rarely dry); albumen none; cotyledons thick and fleshy, with a short radicle.

[2] ANDREWS, E. C., The development of the natural order Myrtaceae. Proc. Linn. Soc. N.S. Wales **38**:529–568. 1913.

From the character of cretaceous climates this or some other theoretical prototype flourished in a mesophytic environment. Among modern groups the nearest approach to this theoretical stock is furnished by the Myrtoideae which are fleshy fruited, most numerous in species, and widely spread in the equatorial regions of the world, with over 75 per cent, however, confined to America. The existing Myrtaceae with capsular fruits, representing the extreme of specialization in the family are Australian, while the Chamaelaucieae, standing in an intermediate position between the two preceding groups, are almost wholly confined to Western Australia.

These are the facts of modern distribution. Their interpretation may be various. ANDREWS (*op. cit.*), from a study of the present distribution, geologic climates, and the geological history of the Australian region, concludes that the Leptospermoideae originated from the Myrteae, and that the cretaceous forms were widespread, which latter was undoubtedly the case. He is convinced also that before the separation of Australia from the Asiatic mainland fleshy fruited forms found themselves in a region of warm moist climate, but relatively poor soil, and that it was this edaphic factor that was the principal stimulus to the differentiation of the Leptospermoideae, which with the exception of the genus *Metrosideros* Banks show adaptations to poor soil and temperate or dry climates, and this exception explains the relatively wide distribution of *Metrosideros* from Asia to the Fiji Islands. The *Eucalyptus* forms, according to the view of this student, were derived from *Metrosideros* after the separation of New Caledonia from Australia and the latter continent from Asia. To support this latter point ANDREWS is obliged to consider all of the cretaceous identifications of *Eucalyptus* and all of the tertiary identifications outside of Australia as equally misleading. With regard to the presence of *Eucalyptus* in North America I think this contention to be not unlikely, for although in accordance with paleobotanical usage I have identified numerous forms of *Eucalyptus* in the North American Upper Cretaceous, I have long thought that these leaves represented ancestral forms of *Eugenia* or *Myrcia*, but have hesitated suggesting any change based merely on personal opinion and also from a consideration that such change in nomenclature is undesirable at the present time from the standpoint of stratigraphic paleobotany, which in this country, at least, is a most useful handmaid of geology.

The supposed cretaceous fruits of *Eucalyptus* have long since been shown to represent *Dammara*-like forms, and in my studies of the tertiary floras I have refrained from referring any of the numerous and unquestionable myrtaceous leaves to the genus *Eucalyptus*. Regarding the possible occurrence of *Eucalyptus* in the Tertiary of Europe, I am not sure that all of the identifications of HEER, UNGER, ETTINGSHAUSEN, and others are erroneous. Certain remains considered as *Eucalyptus* fruits by these authors seem very convincing from the published figures, and furthermore there is not the slightest doubt that the other great Australian alliance of the existing flora, the Proteaceae, was represented in both Europe and America during the Cretaceous and the Tertiary. There is an additional argument against the cretaceous radiation and the paleobotanical determination of *Eucalyptus* which is furnished by the great persistence in the modern forms of the peculiar juvenile, opposite, cordate, sessile, and horizontal leaves, a feature which must represent an ancestral character of long standing before the evolution of the falcate leaves of the genus with twisted leaf-stalks and other xerophytic features.[3]

I have dwelt at some length on this question because of its phylogenetic importance and the possible bearing of the American lower eocene floras on this point. In considering the morphology of the existing species, *Eugenia* has many claims to be considered the most primitive, although *Myrcia* is almost equally old and is certainly closely related to *Eugenia*. Among the numerous cretaceous fossils from North America now referred to *Eucalyptus* there is not a single one that does not exhibit characteristic features of *Eugenia* or *Myrcia*, especially of the latter, a fact greatly impressed on me in handling a large amount of recent material during my study of the American tertiary forms.

[3] See DEANE, H., Observations on the tertiary flora of Australia. Proc. Linn. Soc. N.S. Wales. 15:463–475. 1900; and CAMBAGE, R. H., Development and distribution of the genus *Eucalyptus*. Presidential address, Jour. Proc. Roy. Soc. N.S. Wales, 1913.

In the lower eocene flora of the Mississippi embayment region there are six well marked species of *Myrcia* and four nearly equally well marked species of *Eugenia*, as well as a single species of *Calyptranthes*. The latter genus appears also to be represented in recent collections from the Oligocene of the Isthmus of Panama. Without pursuing the subject beyond the known facts, confessedly meager, and noting the presence in our lower eocene flora of numerous Combretaceae based upon leaves, flowers, and fruits, and a representative of the great tropical family Melastomaceae, largely American in the existing flora, both of which are families closely related morphologically to the Myrtaceae, it would seem that the known facts, as well as the law of probabilities, suggest America as the original home of the family. That in its early deployment it reached Europe, either by way of Asia or the North Atlantic plateau, early in the Upper Cretaceous, and became cosmopolitan before the close of the Cretaceous seems a most probable hypothesis. During the late Tertiary this ancestral stock, which largely coincided with the existing subfamily Myrtoideae, was forced to withdraw from temperate North America to the American tropics, where it had originated and to which it has since been so largely confined.

The types peculiar to the Australian region represent the relics of the cretaceous radiation with numerous new types evolved on that continent in the manner that ANDREWS has suggested, and at a comparatively recent date geologically. This is exactly the reverse of the hypothesis proposed by DEANE (*op. cit.*), but one that accords far better not only with the facts of geologic history, but also with those of existing distribution.

All of the American lower eocene forms are coastal types closely related to existing American species of similar habitat.

About 150 fossil forms have been referred to the family Myrtaceae, one-third at least having been described as species of *Eucalyptus*. At least half of these occur in the Cretaceous of all parts of the world, but particularly throughout the Northern Hemisphere. They are especially well represented in North America, and the possibility that they are ancestral forms of *Myrcia* or *Eugenia* has already been pointed out. A similar widespread distribution but less specific variation characterizes the eocene forms that have been referred to *Eucalyptus*. The oligocene records are all European and the miocene records include both Europe and Asia.

The genus *Myrtus* L. has about 24 fossil species, all European, the majority being almost equally divided between the Oligocene and the Miocene. The oldest forms are early eocene, but the form-genus *Myrtophyllum* Heer has several upper cretaceous species in Europe, America, and Australia, as well as tertiary species in Europe, Asia, and South America.

The genus *Myrcia* DC., so well represented in the Lower Eocene (WILCOX) of our southern states, has species in the Middle Eocene (Claiborne) of the Mississippi embayment area, in the Oligocene (Vicksburg) of Louisiana, and in the European Oligocene. There are four species in the early Tertiary (Eocene or Oligocene) of Chile, one in the Tertiary of Ecuador, and one in the Pliocene of Brazil.

The genus *Eugenia* Linn., also prominent in our lower eocene flora, has its oldest known species in the Dakota sandstone (Upper Cretaceous) of the Rocky Mountain area. It is represented in Europe throughout the Tertiary from the Lower Eocene to the Pliocene, and is recorded by ENGELHARDT from the Tertiary of Ecuador.

The genus *Myrciaria* Berg, often included in *Eugenia*, has about 60 existing species, all American, and found in the area extending from the West Indies to Brazil and Peru. It is represented, according to ENGELHARDT, in the Tertiary of Ecuador.

The genus *Callistemon* R. Brown has been identified in both the Upper Cretaceous and the Tertiary of Europe, and no less than 25 fossil species have been referred to the genus *Callistemophyllum* Ettingshausen. These include upper cretaceous forms in both America and Europe; eocene or oligocene forms in Greenland; and numerous oligocene and miocene species in Europe and Australia.

The genus *Metrosideros* Banks, with an existing species in South Africa, another in the Sunda Islands, and 18 or 20 species in Australia or Polynesia, has 8 or 10 fossil species. The oldest, probably an erroneous identification, is recorded from the Atane beds (Upper Cretaceous) of Greenland. There are 4 species in the Oligocene of Southern Europe and 2 species in the Miocene of that continent.

Leptospermum Forster, *Leptospermites* Saporta, and *Leptospermocarpum* Menzel have been identified from the Upper Cretaceous and Tertiary of Europe. *Tristania*-like fruits have been described as *Tristanites* by SAPORTA from the Lower Miocene of France and by KITSON from the Miocene of Australia. The genus *Psidium* Linn., with about 100 existing species in the West Indies and Mexico, is represented in Chile by an early tertiary species.

It will be seen from the foregoing enumeration that the facts of recent distribution lend support to the thesis of origin which is put forward, and this conclusion is not negatived but supported to a considerable extent by the confessedly meager evidence available in the geological record as at present known.

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